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ABSTRACT

To determine the effect of purse-seine fishing on the Atlantic menhaden (*Brevoortia tyrannus*) population, we analyzed data from 1955–69 on fishing activity and catches. Changes in fishing efficiency necessitated establishment of an abstract effort unit, the 1965 vessel-week. Catch per unit of effective effort in 1965 was one-fifth that of 1955. Our instantaneous natural mortality rate (M) estimate was 0.37. At the current recruitment age, 1.5 years, reducing F, instantaneous fishing mortality, to about 0.8 would slightly decrease the yield per recruit, but would increase the spawning stock and ultimately allow annual catches of 400,000–500,000 metric tons, the maximum sustained yield.

INTRODUCTION

Landings of Atlantic menhaden, *Brevoortia tyrannus*, have declined precipitously in recent years. Fishing and changes in the environment are possible causes of the decline. This study investigates the effect of fishing on the stock. Henry (1971) reviewed much of the data and investigated some aspects of the fishery.

Records of the annual catches and fishing effort are available since 1941 (Table 1) (Nicholson[1]). The landings show a dramatic rise since 1941 and then a decline typical of many expanding commercial fisheries. The age composition of the catch since 1955 (Table 2) is derived from an extensive catch sampling program (June and Reintjes, 1959). These data are the basis for our analysis.

Since most evidence from tagging (Dryfoos, personal communication) and analyses of the age and size distributions (Nicholson[2,3]) indicates one commercially exploited stock of Atlantic menhaden, our investigation presumes this population structure.

AN ADJUSTMENT OF THE EFFORT STATISTICS

Relating dynamics of an exploited fish population to fishing intensity requires knowledge of units of effective effort expended in the fishery. Units of effective effort are those of which a unit increase in effort causes a proportional increase in the fishing mortality rate (F). Great technical innovations in the fishing fleet have impeded precise analysis of the relation between fishing effort and fishing mortality. Power blocks, fish pumps, increase in airplane search time, and nylon nets caused increased effectiveness of the observed unit of effort, the vessel-week (a vessel week is 1 week of activity in the fishery by one vessel) (Nicholson[1]). Other factors acted to increase effective effort in recent years. Foremost of these is a shift of effort to geographic areas where fish were more concentrated. Long term averages of the catch per vessel week (in numbers) are greater in the South Atlantic and Chesapeake Bay and much less in the North and Middle Atlantic and the North Carolina fall fishery. The present fishery exists almost entirely in the South Atlantic and Chesapeake Bay, areas where a unit of effort catches more fish than in other areas. Also we suspect that menhaden are disproportionately more vulnerable when the population is small. While this hypothesis is unprovable with present data, the phenomenon could easily result from density-related behavior changes. So for several reasons, despite an overall decrease in the number of effort units, fishing mortality has not decreased proportionately.

Lacking quantitative measures of the increase in effectiveness of the vessels, we adjusted effort so that the catchability coefficient (q, the fraction of fishing mortality caused by

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[1] Unpublished manuscript, William R. Nicholson, Changes in catch and effort in the Atlantic menhaden fishery, 1940–1968.

[2] Unpublished manuscript, William R. Nicholson, Movements of Atlantic menhaden as inferred from changes in length-frequency distributions.

[3] Unpublished manuscript, William R. Nicholson, Population structure and movements as inferred from back-calculated length frequencies.

TABLE 1.—*Annual catch and effort in the menhaden fishery*

Year	Weight landed	Effort
	Metric tons	*Vessel weeks*
1941	277.9	1,683
1942	167.2	1,233
1943	237.2	1,123
1944	257.9	1,317
1945	295.9	1,496
1946	362.4	1,588
1947	378.3	1,759
1948	346.5	1,928
1949	363.8	2,162
1950	297.2	1,681
1951	361.4	1,803
1952	409.9	1,747
1953	593.2	2,076
1954	608.1	2,173
1955	641.4	2,499
1956	712.1	2,572
1957	602.8	2,455
1958	510.0	2,229
1959	659.1	2,652
1960	529.8	1,999
1961	575.9	2,292
1962	537.7	2,271
1963	346.9	2,277
1964	269.2	1,839
1965	273.4	1,800
1966	219.6	1,435
1967	193.5	1,346
1968	234.8	1,228
1969	161.4	1,003

one unit of effort) was the same for all years. Instantaneous fishing mortality rate (F) is related to fishing intensity (f, equal to observed effort in our analysis) by:

$$F = qf$$

(Terminology and notation is that of Beverton and Holt, 1957).

Since F increased, as we show below, and the observed number of units did not, then unit efficiency (q) increased. From our estimates of numbers of fish caught at each age (Table 2), we obtained maximum estimates

TABLE 3.—*Annual age-specific exploitation rates (u), and maximum instantaneous fishing mortality rates (F_{max})*

Year	Age 2	3	4	5	Mean u_{max}	F_{max}
1955	.71	.73	.61	.51	.64	1.02
1956	.87	.76	.45	.78	.72	1.26
1957	.91	.72	.70	.74	.77	1.46
1958	.75	.53	.46	.51	.56	0.83
1959	.86	.71	.52	.57	.66	1.09
1960	.57	.55	.64	.79	.64	1.01
1961	.64	.71	.31	.51	.54	0.78
1962	.79	.80	.87	.72	.80	1.58
1963	.83	.91	.83	.87	.86	1.97
1964	.83	.90	.90	.86	.87	2.06
1965	.77	.89	.93	.95	.88	2.16

of the exploitation rate (u in Table 3). Since year classes are not fully represented in the fishery until age 2 and often disappear after age 5, we estimated exploitation rates for ages 2 through 5.

$$u_{ij} = C_{ij}/\sum^{k} C_{ij}$$

where u_{ij} = the maximum exploitation rate for age i in year j

C_{ij} = the catch of age i fish in year j

k = maximum age represented in the landings

$\sum^{k} C_{ij}$ = the virtual population (Ricker, 1958) of a year class in year j.

Average age specific exploitation rates ($\bar{u}$) for each year from 1955 through 1965 (Table 3, column 6) were converted to maximum estimates of fishing mortality (F_{max}):

$$\bar{u} = 1 - \exp(-F)$$

TABLE 2.—*Age composition of Atlantic menhaden in landings by purse seiners, 1955–69*

Year	Weight of landings	Age in years[1] 0	1	2	3	4	5	6	7	8–10	Total
	Metric tons	*Millions of fish*									
1955	641,400	761.0	636.5	1,045.6	265.5	300.4	35.3	9.5	1.8	0.6	3,056.2
1956	712,100	36.4	2,078.5	902.6	318.0	45.2	152.4	28.9	6.7	2.0	3,570.7
1957	602,800	300.8	1,596.5	1,348.3	96.5	70.9	40.4	37.0	4.3	1.2	3,495.9
1958	510,000	106.1	859.5	1,625.1	71.9	17.3	15.9	9.1	4.9	0.4	2,710.2
1959	659,100	11.4	4,032.6	821.9	382.7	33.6	11.7	12.3	4.4	1.7	5,312.3
1960	529,800	72.2	281.0	2,207.9	75.0	101.2	24.6	7.4	2.3	0.6	2,772.2
1961	575,900	0.3	832.4	502.3	1,207.1	19.2	29.8	3.1	0.8	0.2	2,595.2
1962	537,700	51.6	519.8	831.8	221.0	421.9	30.6	24.5	2.8	0.6	2,104.6
1963	346,900	84.6	717.8	640.7	199.7	47.0	53.3	10.3	3.5	0.6	1,757.5
1964	269,200	315.7	704.6	578.4	120.7	18.9	8.3	7.7	1.3	0.3	1,755.9
1965	273,400	127.2	820.5	389.2	102.2	12.6	1.9	1.3	0.6	0.1	1,455.6
1966	219,600	303.8	421.8	412.8	106.1	12.0	0.9	0.1	0.1	—	1,257.6
1967	193,500	19.2	522.7	340.9	110.8	8.0	0.6	—	—	—	1,002.2
1968	234,800	68.9	382.1	571.4	183.9	22.9	1.9	—	—	—	1,231.1
1969	161,400	308.4	450.6	141.0	29.9	1.6	0.2	—	—	—	931.7

[1] Age shown is the number of annuli.

TABLE 4.—*The adjustment of effort from the relative catchability coefficient (q)*

Year	Observed vessel weeks	q	Relative q	Effective effort
1955	2,499	.00041	.338	845
1956	2,572	.00049	.404	1,039
1957	2,455	.00059	.491	1,205
1958	2,229	.00037	.308	687
1959	2,652	.00041	.340	902
1960	1,999	.00051	.419	838
1961	2,292	.00034	.285	653
1962	2,271	.00070	.579	1,315
1963	2,277	.00086	.707	1,610
1964	1,839	.00112	.932	1,714
1965	1,800	.00120	1.00	1,800

The last year for which we could obtain an exploitation rate for 5-year-old fish was 1965, since after 1965 there were no fish older than five in our samples. Consequently this method of adjusting effort is valid only for the period 1955 to 1965. Dividing F by f, the observed effort, yields an index of q, the catchability coefficient. This coefficient, the fraction of F caused by one unit of effort, has increased threefold during this 11-year period, indicating that a vessel week of fishing in 1965 killed 3 times the fraction of the population that a vessel week in 1955 did. Multiplying the effort observed each year by relative change in q or dividing F_{max} in each year by the index of q (.0012) for the base year 1965 estimates the number of units of effective effort applied each year (Table 4). Effective effort has doubled during this period even though nominal effort has declined.

STOCK-EFFORT RELATION

Changes in catch per unit of effective effort, an index of stock abundance, indicate a five-

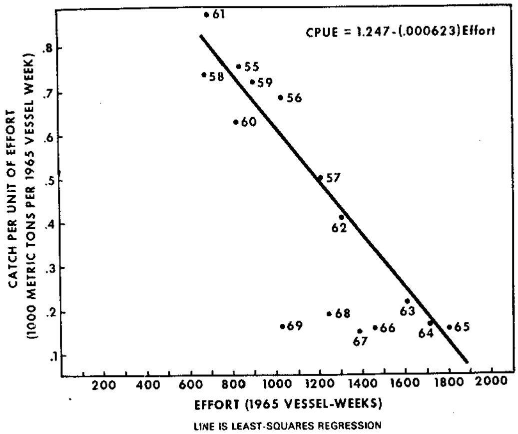

FIGURE 1.—The relationship of the annual catch per unit of effective effort to the effective effort for 1955–65. Data from Tables 1 and 4. Points for 1966–69 are unadjusted; see text.

fold decrease of total stock (Fig. 1) through 1965. The four most recent years 1966–1969, are plotted in this figure for information only, since the effort units have not been adjusted. We feel that any adjustment would cause these points to shift downward and to the right nearer the line (i.e., effective effort has continued to increase; certainly older age classes have continued to drop out of the fishery). If we assume that effort in these years is as efficient as in 1965, then these four points imply that the population has not yet responded to a reduction in effort. This delayed response could be due to the large reduction in the size of the spawning stock (Table 7).

The negative linear relation of stock size and effective effort suggests overfishing. An exponential relationship is typical of many exploited marine fishes, and so long as only mature individuals are harvested, it is difficult to exterminate the population (Fox, 1970).

TABLE 5.—*Calculation of total instantaneous mortality rate, Z, from the catch per unit of effective effort (CPUE)*

Year	Effective effort	CPUE Ages 2	3	4	Weighted Z
1955	845	1.40	1.98	.88	1.50
1956	1,039	2.38	1.65	.26	1.55
1957	1,205	2.37	1.16	.93	1.51
1958	687	1.72	1.03	.66	1.17
1959	902	2.32	1.25	.24	1.36
1960	838	.36	1.12	.98	0.83
1961	653	1.52	1.75	.23	1.29
1962	1,315	1.63	1.75	2.27	1.84
1963	1,610	1.73	2.42	1.81	2.03
1964	1,714	1.78	2.31	2.30	2.13
Inverse of Standard deviation		1.67	2.01	1.25	

TABLE 6.—*The yield in grams per recruit at various fishing mortalities for four ages at first recruitment*

Instantaneous fishing mortality	Age of recruitment *1.5*	*2.0*	*2.5*	*3.0*
0.2	77	72	66	59
0.4	105	102	96	88
0.6	116	115	110	102
0.8	121	122	118	111
1.0	122	125	123	116
1.2	123	127	125	119
1.4	123	128	127	122
1.6	123	129	129	123
1.8	122	129	130	125
2.0	122	130	130	126

TABLE 7.—*Estimation of spawning stock (S) and recruitment (R) for M = 0.37*

Year	Z	F	u_S	$Catch_S$	S	u_R	$Catch_R$	R
				Millions of fish			*Millions of fish*	
1955	1.51	1.14	.59	613.0	1,039.0	.45	636.5	1,414.4
1956	1.55	1.18	.60	553.2	922.0	.46	2,078.5	4,518.5
1957	1.51	1.14	.59	250.3	424.2	.45	1,596.7	3,548.2
1958	1.17	.80	.47	119.4	254.0	.35	859.2	2,449.7
1959	1.36	.99	.54	446.4	826.7	.41	4,032.6	9,835.6
1960	0.82	.45	.31	211.2	681.3	.22	281.0	1,277.3
1961	1.29	.92	.52	1,260.2	2,423.5	.39	832.4	2,134.4
1962	1.84	1.47	.67	701.4	1,046.9	.53	519.8	980.8
1963	2.03	1.66	.71	314.4	442.8	.58	717.8	1,237.6
1964	2.14	1.77	.73	157.2	215.3	.60	704.6	1,174.3
1965	—	—	.60[1]	118.7	197.8	.47[1]	820.5	1,745.7
1966	—	—	.60	119.3	198.8	.47	421.8	879.4
1967	—	—	.60	119.4	199.0	.47	596.1	1,268.3
1968	—	—	.60	208.9	348.2	.47	382.1	813.0
1969	—	—	—	31.7	52.8	.47	377.3	802.7

[1] From 1965 through 1969 u_S and u_R are means of previous years.

However, menhaden numbers have declined linearly. A striking aspect of this fishery is the rapid, successive disappearance of older age classes since 1966. Now, more than ever, the bulk of the harvest is immature fish.

The declining stock size has not been compensated by increased growth or recruitment, since the total catch has also declined dramatically (Fig. 2). At least since 1962 the fishery has been operating beyond the peak of the catch-effort curve and has been on a decline typical of biologically overexploited populations. Again, the last four points are unadjusted. The failure of the population to respond in weight could be due also to the collapse of older age classes.

Age specific mortality rates for ages 2, 3, and 4 were calculated (Table 5):

$$Z_{ij} = \log_e (C_{ij}/E_j) - \log_e (C_{i+1}/E_{j+1})$$

where Z_{ij} = the total instantaneous mortality rate for age i fish in year j

C_{ij} = the estimated numbers of age i fish caught in year j

E_j = effective effort in year j (shown in Table 4) (Beverton and Holt, 1957)

For each year from 1955 through 1964 these age specific rates were averaged, each Z_i being weighted by the inverse of the standard deviation of the Z_i's for all years. This gave the most weight to the age specific mortality rate which is least affected by fluctuating year class strength.

Instantaneous natural mortality, M, is estimated by the intercept of a least square regression of Z on effective effort (Fig. 3). Iterating to correct for annual changes in

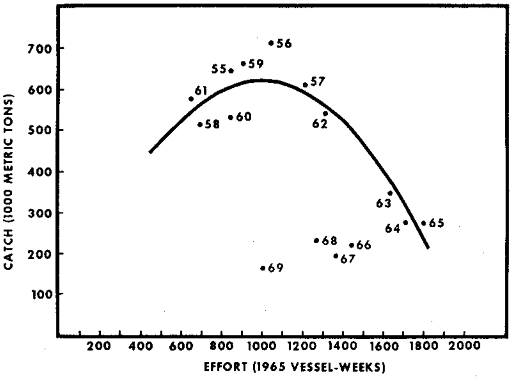

FIGURE 2.—Total catch related to effective effort for 1955–65. Data from Tables 1 and 4. Points for 1966–69 are unadjusted; see text.

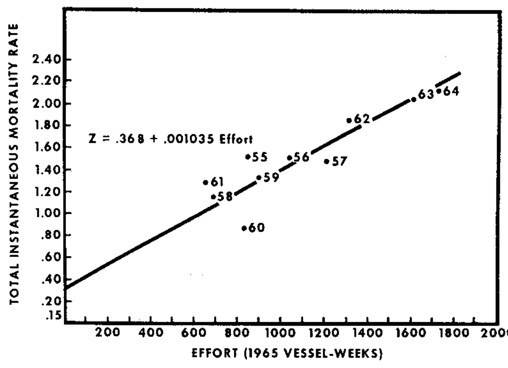

FIGURE 3.—The iterated least squares regression of total instantaneous mortality rate on effective effort.

effort yielded after 3 iterations, an M of 0.37, a value only 0.01 less than that after 2 iterations.

This analysis of mortality does not prove a causal relation between increasing total mortality and observed fishing effort, but only attempts to describe an assumed relation. The method used for adjusting effort caused both the Z's and the effective effort to be determined entirely by the age structure of the catches.

This can be seen from the following simplified algebraic argument (where f( ) means "a function of"):

$Z_j = f(E_j/E_{j+1})$, for a fixed series of age specific catches but:
$E_j = F_{maxj}/q_b$, where q_b = catchability coefficient in base year
so $E_j/E_{j+1} = F_{maxj}/F_{maxj+1}$
and F_{max} = f (only of catches)

An alternative explanation for the apparent increase in total mortality is an increase in the natural mortality rate. Although we have not investigated this hypothesis there is no apparent evidence for the increase of any mortality factor in the menhaden environment, especially a factor which would cause the progressive disappearance of the older age groups.

THE STEADY STATE YIELD PER RECRUIT

The assumption of constant mortality rates and growth parameters during the fishable life span of menhaden, allows calculating the yield per recruit from the dynamic equation of Beverton and Holt.

$$Yw/R = FW_\infty \exp(-M\rho) \sum_{n=0}^{3} \frac{\Omega n \exp[-nk(t'_\rho - t_0)]}{F + M + nK} [1 - \exp - (F + M + nk)\lambda]$$

where λ = the fishable life span = 8.0
t'_ρ = the age at which we impose fishing mortality
ρ = the time spent in the pre-recruit phase.

Length at age data from 257,000 scale samples for males and females, years 1955 through 1969 were fit to the Von Bertalanffy growth curve:

$$l_t = L_\infty (1 - \exp[-K(t - t_0)])$$

where l_t = length at age t
L_∞ = the asymptotic length
K = the rate with which l_t approaches L_∞
t_0 = the theoretical age at which length is zero.

Length was converted to weight by the following empirically determined formula:

$$W_t = .00000676\, l_t^{3.18}$$

The combined sample gave average parameter values of:

$$W_\infty = 830 \text{ g}$$
$$K = 0.391$$
$$t_0 = -0.93$$

These were used in the above yield equation. We chose 0 as the age at which menhaden could be first captured. Imposing four ages at which fishing mortality begins, 1.5, 2.0, 2.5 and 3, gave values for ρ of 1.5, 2.0, 2.5, 3.0, and resulted in the yield values presented in Table 6. At the current recruitment age, 1.5, it does not pay to fish at a rate greater than about 0.8. For F's greater than 0.8 there is some gain in harvest by delaying recruitment to age 2.0. This is contrary to a widely held notion that if menhaden are not caught at a young age there will be great losses due to natural mortality. Either decreasing F, given the current recruitment age, or increasing recruitment age will not only be economically advantageous but should increase the spawning stock.

STOCK-RECRUITMENT RELATION

An important change in the menhaden stock, however, which has grave implications for the fishery, is the precipitous decline in both the spawning stocks and the size of resultant year classes. A description of the relationship between stock and recruitment is useful for examining the current coincidence of reduced spawning stock and decreased recruitment, and for predicting the fate of the fishery under different fishing regimes.

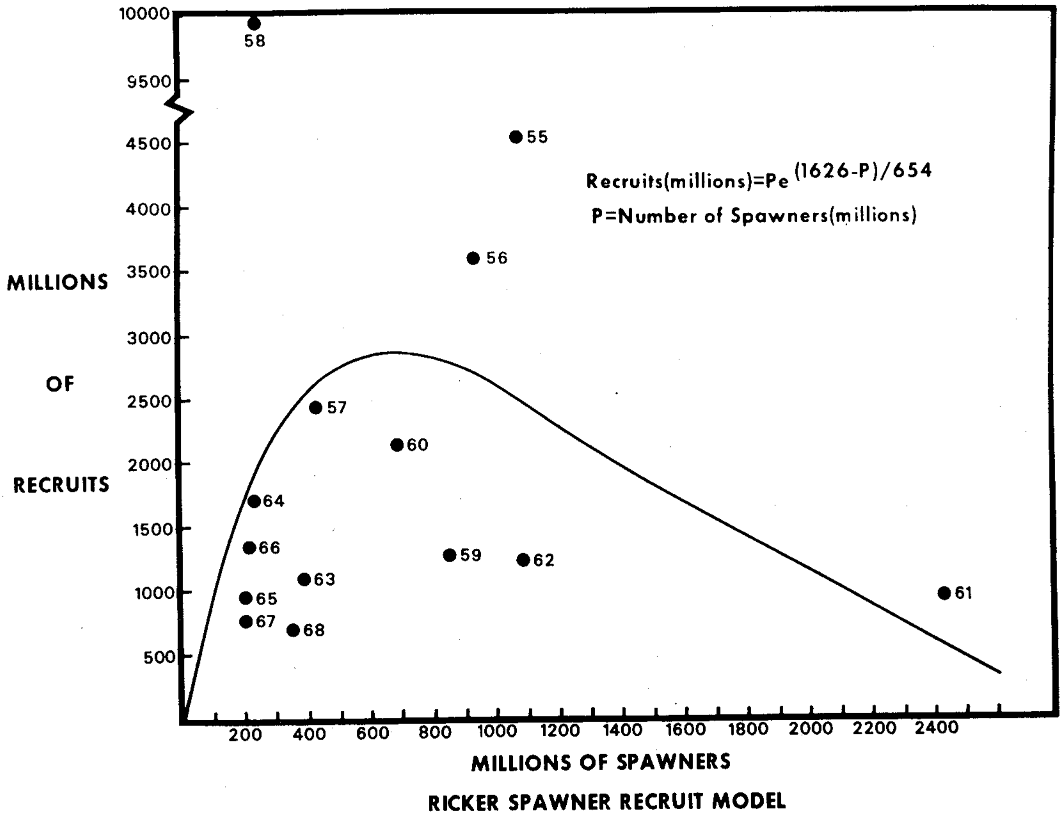

FIGURE 4.—Ricker spawner-recruitment model.

Ricker's (1958) stock-recruitment model, which we have used, states that there is no recruitment with no spawning stock, that some spawning stock (P_m) produces the maximum recruitment, and that, because of density dependent mortality, stocks greater than P_m produce progressively fewer recruits. These characteristics seem compatible with present notions about menhaden, and we used the Ricker model in our analysis.

We obtained the necessary estimates of stock and recruitment from our estimates of the number of fish of each age caught each year, estimates of Z each year, and our estimate of M. Menhaden captured at age 3 and older in year j produce the recruits, age 1 fish, of year j + 1 (Higham and Nicholson, 1964). Knowing for each year Z, M, and consequently, F, we calculated the annual expectation of death from fishing for the spawning stock (S):

$$u_S = F(1 - e^{-Z})/Z$$

Then $$S_j = \sum_{i=3}^{k} C_{ij}/u_S \qquad \text{(Table 7)}$$

where S_j = spawning stock in year j
C_{ij} = catch in numbers of age i in year j.

Since Atlantic menhaden are apparently not fully recruited until they are about 2 years old (June and Reintjes, 1959) and since the exploitation rates (u_{max}) for 1-year-old fish averaged 66% of u_{max} for ages 2 through 5, only 66% of F was applied to obtain u for age 1 fish.

So that:

$$R_j = C_{1j}/u_R \qquad \text{(Table 7)}$$

where R_j = recruitment in year j, and
$u_R = 2F(1 - e^{-Z})/3Z$

Fitting the Ricker model (Fig. 4) yielded an estimate of the stock producing the greatest recruitment, P_m, of 654 million fish. P_m would produce 2.9 billion recruits.

The stock-recruitment model allows prediction of future population structures under different levels of fishing. A Fortran IV simulation program incorporating the Ricker stock-recruitment model, our estimate of M, selected values of F, and weight at age information allowed us to make such predictions. Our predictions depend, of course, on the occurrence each year of the average recruitment for the stock size in question. The variability of the data emphasizes the need for caution in using these projections. Despite this variability our model provides reasonable inferences about the population. Our model's predicted maximum sustainable yield (MSY), 380,000 metric tons, is close to our empirical notion of MSY (from historical data) of about 500,000 metric tons, to lend some credence to the analysis.

The concurrence of extremely small spawning stocks and recruitments in the last 3 years is striking. This concurrence furnishes circumstantial evidence that declining yields have resulted from reduced spawning stock and, possibly, fishing.

Our model indicates that the optimum fishing mortality is 0.80 (Fig. 5). Imposing greater fishing mortality significantly decreases maximum yields and increases the time required to reach the maximum. Fishing at F below 0.8 will achieve greater short term yields but these too level off below the curve for $F = 0.8$. If $F = 0.6$, the cumulative yield achieved by 1983 (where the curves cross) is 3,222,000 metric tons, while the cumulative yield from $F = 0.8$ is 2,749,000 metric tons up to 1983. Delaying harvest for a period of years produces large yields faster. For instance, waiting 2 years and then fishing at 0.6 yields a sum of 3,580,000 tons by 1983. Fishing at $F = 0.8$ after a two year wait yields 3,648,000 tons. If $F = 1.2$, the average value for the period 1955 through 1964, the yield climbs very slowly to 129,000 tons per year after 30 years; while fishing mortalities in excess of 1.2 (which have occurred in recent years) cause collapse of the population.

Our equilibrium catch-effort curve from historic data predicts a yield of 600,000 metric tons while the population-prediction model suggests a yield of only 380,000 metric tons. The catch-effort curve is probably biased upward because of the succession of exceptional year classes in the 1950's. The population-prediction model depends greatly on the spawner-recruitment model, which is insensitive to and dampens the effects of those large year classes. These two yield estimates bracket an historical notion of sustained yield of 500,000 metric tons. These estimates are relatively close together and warn against optimistic appraisal of the menhaden resource as unlimited.

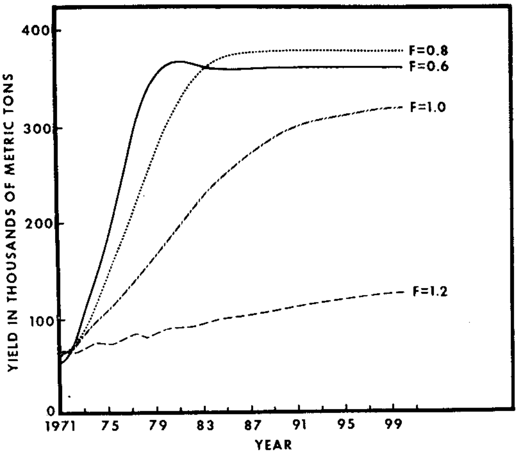

FIGURE 5.—Projected yield achieved from four different fishing mortalities.

CONCLUSIONS

This analysis demonstrates, after accounting for changes in the fishery, a considerable impact of fishing on the resource. The stock is greatly diminished probably as a result of excess fishing, and recovery will occur only if F is diminished. Moreover, after recovery of the population annual catches should be about 400,000–500,000 metric tons. This should insure adequate spawning. To attempt a more precise estimate of MSY would be unrealstic with these data. It must be emphasized that, extensive as our records have now become, the statistics which form this picture of menhaden dynamics represent a small portion of the history of the fishery, and particularly that the catch composition data is available only for the period of declining yields since the peak harvest of 1956. In spite of limitations in the data, a production model for menhaden is needed to help prevent the unnecessary destruction of an industry and a national resource.

ACKNOWLEDGMENTS

This work was possible only because of the efforts of many past and present participants in menhaden research at our laboratory. We wish to acknowledge especially, Mr. William R. Nicholson, who was instrumental in collection of biostatistical data, provided invaluable assistance in formulation of our thoughts on effort, and served as a living sourcebook on the history of the fishery. Dr. Brian J. Rothschild, University of Washington, Seattle, Washington gave helpful suggestions. Much of our work was eased by computer programs written by Mr. John E. Hollingsworth.

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